

Divergent Host Acceptance Behavior Suggests Host Specialization in Populations of the Polyphagous Mite *Abacarus hystrix* (Acari: Prostigmata: Eriophyidae)

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ABSTRACT For phytophagous arthropods, host acceptance behavior is a key character responsible for host plant specialization. The grain rust mite, *Abacarus hystrix* (Nalepa), is an obligately phytophagous, polyphagous eriophyid mite recorded from at least 70 grass species. In this study, the hypothesis that two host populations of this mite (one collected from quackgrass and the other from ryegrass) are highly host-specific was tested using behavioral data. For this purpose, female behavior when exposed to familiar and novel host plants was observed in no-choice cross experiments. Altogether, 13 variables were used to describe mite behavior. Data were subjected to principal component analysis, and host acceptance behavior was subsequently tested with generalized estimating equations (GEE). Distinct variation in female behavior between familiar and novel hosts was observed. Females from neither population accepted novel hosts. This was recorded as significant differences in the occupation of and overall activity on particular plant parts. On their familiar host, females were not active and showed little tendency to move. On novel hosts females were more active and mobile, spending more time walking, running, and climbing on the whole plant surface and showing a tendency to disperse. Other differences in behavior between studied populations were also observed. Thus, the results suggest that mites of these two studied populations (1) differ in their behaviors during plant exploitation and (2) can quickly distinguish between their familiar host and an unfamiliar host used by a conspecific. These findings support the hypothesis of narrow host specialization of ryegrass and quackgrass populations of this highly polyphagous species.

KEY WORDS host acceptance, host races, host specialization, grain rust mite, principal component analysis

For obligately phytophagous arthropods, survival and reproductive success depend on the ability to efficiently find suitable host plants. To maximize reproductive success, phytophagous organisms have to both precisely assess the suitability of their host and subsequently be able to cope with its biotic and physical characteristics (e.g., plant chemical composition, presence of natural enemies). Thus, the adaptation of a plant-feeding arthropod to a novel host must involve both behavioral and physiological traits (Jaenike 1990). Because information about host suitability is usually available to herbivores through chemical and physical cues (e.g., the odor of a preferred host plant, odors from natural enemies and competitors, plant physical structure), or-

ganisms are expected to have evolved the ability to discriminate between these signals and make correct decisions during host selection (Bierbaun and Bush 1990, Dicke 2000).

In the evolution of ecological specialization, characters that directly influence both specialized habitat use and the extent of assortative mating seem to be of particular importance. It has been suggested that behavior has special importance in this process, because behavioral changes could enable the use of a new environment and selection would only act on the morphological and physiological characters subsequently expressed there (Futuyma and Moreno 1988, Caillaud and Via 2000). Thus, for host specialization, behaviors exhibited during host plant choice (i.e., host acceptance or rejection) are of great significance. Furthermore, the positive correlation between specific host plant preferences and both host-specific fitness and positive assortative mating is a key character responsible for host plant specialization (Maynard Smith 1966, Bush 1975).

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In this study, we present behaviors exhibited by two populations of an eriophyoid mite, *Abacarus hystrix* (Nalepa), during the colonization of familiar or novel hosts. The Eriophyoidea is comprised of >3,760 species, all of which are obligate herbivores. Many of these species attack economically important plants, and several of them are vectors of plant diseases (Lindquist et al. 1996). Despite such an important role in agriculture and the environment, knowledge of host specialization in eriophyoid mites is lacking. To fill this gap, testing plant acceptance and performance by measuring a mite's ability to colonize, survive, and reproduce on various hosts is necessary.

The grain rust mite, *A. hystrix*, is a tiny (≈ 0.2 mm in size), four-legged eriophyid mite. It lives on grasses and is widely distributed worldwide. Because of the leaf discoloration it causes and the plant diseases it can transmit (ryegrass mosaic virus [RMV], a serious disease of temperate pastures, and agropyron mosaic virus [AMV], a minor disease of wheat and quackgrass), the mite is considered a significant pest of cultivated grasses (Frost and Ridland 1996). In view of its economic importance, reliable, detailed knowledge of the mite's host specificity is particularly needed. The grain rust mite has been recorded on at least 70 grass species (Frost and Ridland 1996, J. Amrine and E. de Lillo, unpublished data). Individuals are passively dispersed from one host to another by air currents (Nault and Styer 1969). During such dispersal, a mite has no control over which plant species it will land on. If it alights on an unsuitable host, it can either try to disperse again or it will die. Therefore, considering the mode of dispersal and the many host plants recorded for this mite, it has been hypothesized that narrow host plant specialization in *A. hystrix* was not likely to evolve and that the mite should be more successful as a generalist (Sabelis and Bruin 1996). However, recent observations have shown that at least two populations of this mite (found on ryegrass, *Lolium perenne* L., and quackgrass, *Elymus repens* L. Gould, in western Poland) may be highly specialized in their host use and should be regarded as host races. First, significant differences in body shape and overall body size between the two populations have been recorded (Skoracka et al. 2002). Second, these two populations differ significantly in their life history traits, including developmental time, female survival, and ovipositional strategies (Skoracka and Kuczyński 2006a). Finally, females from both populations have significantly reduced fitness (assessed by their survival and fecundity) when reared on each other's host (i.e., on a novel host) (Skoracka and Kuczyński 2006b).

In this study, we used behavioral data to test the hypothesis that these two populations of the grain rust mite are highly specialized host races. In host-changing and no-choice experiments, we attempted to simulate situations that would occur under natural conditions. In the field, when mites are forced to leave their host (e.g., because of plant withering or high mite population density), females, which are mainly responsible for dispersal, climb toward the top of a leaf and lift their bodies to be more exposed to wind (Nault

and Styer 1969). Because an air-borne mite cannot choose where it will land, mites land on hosts more or less at random (Sabelis and Bruin 1996). If highly specialized mites (such as host races) land on a novel host for which their fitness is lower than on the familiar host, their preference for or acceptance of the novel host should also be lower. Given that animal behavior can reflect the degree of habitat acceptance, mites should behaviorally exhibit nonacceptance with respect to relatively unsuitable hosts. To study host acceptance behavior in the grain rust mite, females of two populations (from ryegrass and quackgrass) were infested onto their familiar host (on which their fitness was expected to be high) and onto each other's host (on which their expected fitness was low). In this way, the hypothesis that host races show host preferences positively correlated with host-specific fitness (Maynard Smith 1966, Bush 1975) was tested. Because eriophyoid mites do not exhibit any host location mechanism (Lindquist and Oldfield 1996), determining their host preference is not a relevant measure of host plant selection. Thus, we measured host acceptance instead of strict choice. The same was suggested for other wind-dispersed mites by Byrne et al. (1982) and Agrawal et al. (2002).

Specifically, the aim of this study on the grain rust mite was (1) to give a quantitative and longitudinal description of mite behavior when colonizing novel and familiar host plants, (2) to find a synthetic behavioral measure of host acceptance, (3) to describe longitudinal development of host acceptance behavior based on this measure, and (4) to test if host acceptance behavior differs significantly between familiar and novel hosts.

Materials and Methods

Plant Material. Two grass species, quackgrass, *Elymus repens*, and ryegrass, *Lolium perenne*, were used as experimental plants. These species were chosen because they were known from previous work to differentially influence phenotype and fitness of grain rust mite populations (Skoracka and Kuczyński 2006a, b). Both grass species are perennial, cosmopolitan, and frequently grown. They differ in plant architecture and ecological requirements. Quackgrass has flat, slightly striated leaves with sparse long hairs on the upper leaf surface. It often forms tufts and grows in grasslands, on roadsides, and on abandoned and cultivated lands. It is a serious weed and is difficult to eradicate because of its deep rhizomes, any fragment of which can regrow. Quackgrass is frost-, flooding-, and drought-resistant and tolerates shade and salinity. It prefers a warm climate and grows poorly in saturated soil. It is characterized by low sodium content. It is a good indicator of soils rich in nitrogen and phosphorus. Ryegrass is a clumped grass, with glossy, bare, deeply striated, narrow, and often folded leaves. It is common in grasslands, grass-plots, sport fields, and near airfields. It prefers loamy and subhumid soil and moderate, maritime, and humid climates. Ryegrass does not tolerate low temperatures, standing water, or

constant shade and grows poorly in swampy or sandy soil. It is the most important grass sown in areas with a temperate climate and is used in pasture production (Rose 1989, Chapman 1996).

Ryegrass seeds and quackgrass rhizomes were obtained in October 2003 from two separate study plots in Poznań, Poland (ryegrass: 16°52.5' E, 52°26.5' N; quackgrass: 16°53.0' E, 52°24.5' N), and germinated in boxes with loamy and sandy soil, respectively. Plants were kept at room temperature and exposed to artificial light for 19 h/d. The boxes were covered with nylon taffeta that was fastened to the wooden frame to protect plants from infestation by arthropods or fungi. When fully grown, these plants were transplanted to pots to prepare stock mite colonies and experiments.

Stock Colonies of Mites. Stock colonies of mites were established with mites collected in November 2003 from quackgrass and ryegrass plants from the same study plots described above. Sampled plants were transported to the laboratory where adult females of *A. hystrix* were transferred to the laboratory-grown plants to establish the stock colonies. Females from quackgrass were transferred to uninfested quackgrass plants (hereafter Q-population), and females from ryegrass were transferred to uninfested ryegrass plants (hereafter R-population). [In previous work (Skoracka and Kuczyński 2006a, 2006b), these two populations have been known as L (ryegrass) and A (quackgrass).] Mite specimens were transferred under a stereomicroscope using an eyelash glued to a preparatory needle. Females of *A. hystrix* can be distinguished from other species or conspecific males and immatures by the presence of a dorsal ridge or by the body shape and dimensions, respectively. A few specimens from each colony were mounted in slides and are deposited in the Department of Animal Taxonomy and Ecology, Adam Mickiewicz University, Poznań, Poland. The mite colonies (Q and R) were maintained in separate controlled environment chambers (19°C, 85 ± 1% RH; 17:7–18:6 L:D). After 2 mo, females from the stock colonies were randomly chosen for use in the no-choice host-acceptance tests.

Experimental Setup. Shoots of the laboratory-grown grasses were transplanted to pots with one shoot of grass per pot. Each shoot was left with only one medium-sized leaf (the experimental leaf), whereas the others were cut off. Leaves that sprouted during the experiment were called new leaves. Female behavior was observed for Q-population and R-population separately when they were infested on the same grass species as in their stock colony, i.e., the familiar host plant, or on the other grass species (a novel host plant). For this purpose, females of each of the two examined populations were transferred from the stock colony to a familiar host plant (control group) or to a novel host plant (experimental group). Four combinations (groups) were tested: (1) QQ, females from quackgrass transferred to quackgrass (familiar host); (2) QR, females from quackgrass transferred to ryegrass (novel host); (3) RR, females from ryegrass transferred to ryegrass (familiar host); (4)

RQ, females from ryegrass transferred to quackgrass (novel host; Fig. 1).

An experimental unit was defined as a sequence of observations of a group of females on a single plant. Each sequence was initiated by placing 13–17 females on one experimental leaf. Individual mites were assumed to not interact with each other at these densities. After 15 min, the leaf was checked again to count the number of females that had successfully settled on the leaf. This was the first observation. Each plant was subsequently inspected 10 times at 8-h intervals. Thus, a single sequence lasted 80 h with 11 observations. This duration was sufficient to obtain behavioral data. Near the end of this interval, the survival of females on novel hosts decreased significantly (Skoracka and Kuczyński 2006b). The total number of females tested was $n = 362$; numbers of females for each group separately were as follows: QQ, $n = 80$ (on six plants); QR, $n = 102$ (six plants); RR, $n = 75$ (seven plants); RQ, $n = 105$ (five plants).

Altogether, 13 variables (characterized below) were used to describe the mites' behavior, as well as the part of the plant occupied. During each inspection each female was observed for 0.5 min, during which time its behavior and position on the plant and leaf were recorded. The number of females assigned to each category was counted (scan sampling).

All experiments were conducted in controlled environment chambers (19°C, 85 ± 1% RH; 17–18/6–7 L:D), with each group conducted concurrently but separately.

Description of Variables: Behavior. Behavior and location of female mites were described based on earlier work (Krantz 1973, Gibson 1974, Westphal and Manson 1996; A. Skoracka, unpublished data). Behaviors observed were as follows. (1) Lying (LYI), female lies immobile in the leaf furrow adhering to the leaf surface, positioned along the leaf length. This is a typical feeding or resting position of eriophyoid mites indicating the plant's acceptability. Duration of mite feeding varies from 1 min to ≈1 h, after which the mite leaves the feeding site to locate another one. (2) Sitting (SIT), female sits (i.e., has a slightly bent opisthosoma, not adhering to the leaf surface) and touches the leaf surface using empodium claws. This position is displayed during probing and checking the suitability of a site for feeding. (3) Walking (WAL), female moves slowly over the host surface, stopping momentarily and continuing. Walking is usually undertaken for the purpose of finding a suitable feeding site. Gibson (1974) reported that adults move at 2.6–0.4 mm/min on a ryegrass leaf at an ambient temperature of 25°C. (4) Running (RUN), female moves quickly and does not stop. (5) Dispersing (DIS), female displays a dispersal position, i.e., lifts its opisthosoma up, stands erect waves its legs. This position is displayed when unfavorable conditions on the host plant appear or when suitable conditions for aerial dispersal occur (e.g., temperature, wind velocity) (Lindquist and Oldfield 1996).

Description of Variables: Location. Females were found on the following parts of the plants: (1) inside the furrow on the upper side of the experimental leaf

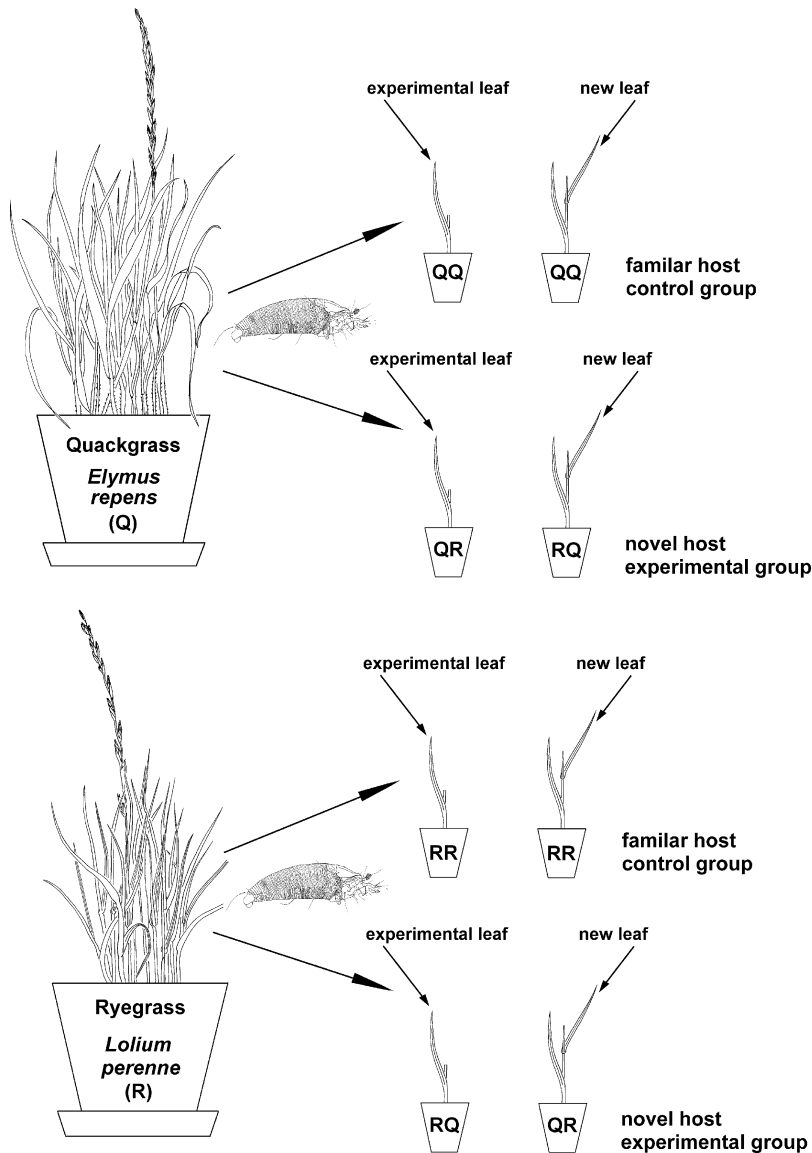


Fig. 1. Design of no-choice cross experiments.

(i.e., the leaf on which mite was originally placed) (FUE); (2) on the upper side of the experimental leaf (but not in the furrow) (USE); (3) on the lower side of experimental leaf (LSE); (4) on the lower site of a newly sprouted leaf (LSN); (5) on the upper side of a newly sprouted leaf (USN); (6) on the stem (shoot) below the base of experimental leaf (STE); (7) on the leaf margin (MRG); (8) on the leaf ligule or base (LIB).

On their familiar hosts, mites usually occur in furrows on the upper leaf surface. Other sites are less suitable for mite feeding, with the stem, margin, and lower leaf surface being the least suitable.

Data Analysis: Data Reduction. Altogether, 13 variables were used to describe behavior (5 types of behavior and 8 parts of the host plant occupied). During

scan sampling, the number of females showing a given type of behavior and occupying a given place was recorded. During data preprocessing, these values were converted into percentages by dividing them by the number of females present at the time of sampling. Variables describing behavior and site preferences were not independent. Moreover, simultaneous tests of between-group differences in a set of 13 variables would dramatically rise the probability of type I error (Manly 2004). To avoid this, principal component analysis (PCA) was used as a way of data compression. This method projects the original data into new space in reduced dimensions, retaining the majority of information. One advantage of such projection is orthogonality—i.e., derived components are independent. Components are linear combinations of

Table 1. Loadings of the principal components of behavioral and location variables

Variable	PC1	PC2	PC3
Behavioral			
LYI—lying	-0.59	-0.53	-0.12
SIT—sitting	0.03	0.04	-0.17
WAL—walking	0.37	0.29	0.34
RUN—running	0.14	0.15	-0.07
DIS—dispersing	0.04	0.04	0.02
Location			
FUE—in furrows, upper side of EL	-0.53	0.61	-0.20
USE—not in furrows, upper side of EL	0.07	0.15	-0.16
LSE—lower side of EL	0.03	-0.14	-0.09
LSN—lower site of NL	0.15	-0.14	0.07
USN—upper side of NL	-0.18	-0.18	0.81
STE—stem	0.38	-0.37	-0.32
MGR—leaf margin	0.07	0.07	0.06
LIB—leaf ligulae or base	0.01	-0.01	-0.01
Eigenvalues	5.16	1.69	1.58
Cumulative percent of variance	60.2	75.8	86.4

EL, experimental leaf; NL, new sprouted leaf.

Detailed descriptions of variables can be found in the Material and Methods.

original variables and can be interpreted relatively easily. This gives the opportunity to describe and analyze complicated and inherently multivariate processes using simple and biologically meaningful measures.

Data were summed over all units of the same type of experiment, giving a matrix of 40 records (4 experimental groups times 10 time intervals in each group) and 13 variables. PCA scores estimated on these data were used to calculate PCA values in the original data set (i.e., on observations not pooled). PCA was performed to reduce dimensionality in the data and to find an index capable of measuring host acceptance behavior. At this stage of analysis, because no statistical inference was made, all observations were treated as independent.

Behavioral Measure of Nonacceptance. The interpretation of principal components was done on the basis of factor loadings. The highest loadings of the first component are associated with variables describing mite activity and mobility on unusual sites of the plant. The lowest loadings are associated with variables describing mite inactivity and occupation of the most suitable sites of the plant (Table 1). Thus, this component can be interpreted as a measure of behavioral nonacceptance. It expresses the contrast between the amount of time spent in active exploration of unfamiliar space and the amount of time spent resting and feeding in a suitable habitat.

The second component is an index of mite activity within its usual habitat. Positive loadings are associated with variables describing a tendency to walk and run on the experimental leaf. Negative loadings are associated with variables describing inactive behavior on the other parts of the plant (Table 1).

The third component measures the tendency to move toward the upper part of the plant. Positive loadings are associated with variables describing walking activity on newly sprouted leaves. Negative load-

ings are associated with variables describing inactive behavior on the experimental leaf and lower parts of the plant (Table 1).

The above described components explain 60, 16, and 10% of the total variance, respectively. Only the first component was used to describe longitudinal development of nonacceptance behavior (NAB hereafter) and to test differences between control (familiar host) and experimental (novel host) groups. The second and the third components measure behavior that is not directly related to host acceptance and they were excluded from further analysis.

Testing Differences Between Control and Experimental Groups. The development of NAB during experiments and differences between experimental and control groups were tested using generalized estimating equations (GEE) analysis with a log-link function and Poisson distribution of errors (Liang and Zeger 1986). Two separate models were constructed, one for each host population (i.e., QQ was tested against QR and RR against RQ). The main question we addressed was to test differences in longitudinal development of NAB. To achieve this, the time variable was nested within each experimental group. Moreover, NAB changes curvilinearly over time. Some trials were done using natural spline smoothers to model these relationships, but a second-order polynomial was used as a sufficient parametric approximation. For all computations, the S-PLUS software was used (S-PLUS 7.0; Insightful 2005).

Results

Longitudinal Description of Mite Behavior. Patterns of the change of the behaviors of the four studied groups of *A. hystrix* were seen in the five behavioral variables studied throughout the duration of the experiment (Fig. 2). Both control groups (QQ, RR) showed similar patterns to each other, whereas both experimental groups (QR, RQ) also showed similar patterns. Considerable differences between control and experimental groups were observed within four variables: lying, walking, running, and dispersing. The largest group of females from the control groups showed low activity and low mobility and spent their time lying. Females from the experimental groups were more active and mobile and spent their time walking, running, and displaying dispersal behavior. However, the activity of females in the experimental groups decreased throughout the experiment, whereas the percentage of lying females increased.

Patterns of the change of the occupation of plant parts by the grain rust mite were seen throughout the duration of the experiment in the eight location variables studied (Fig. 3). Control groups (QQ, RR) showed similar patterns for seven of the eight variables studied. They differed in the occupation of the lower side of the experimental leaf (LSE). Experimental groups (QR, RQ) showed similar patterns within five among eight variables studied. They differed in the following variables: LSE, USE, and STE. The most

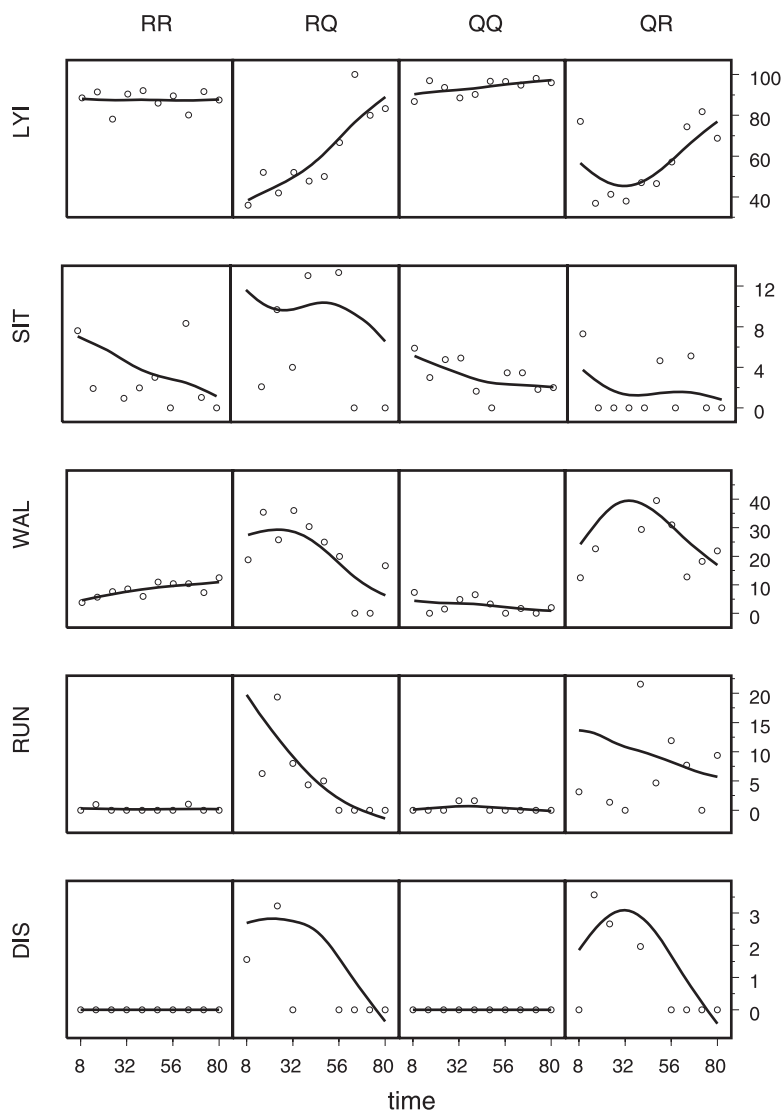


Fig. 2. Longitudinal changes in mite's behavior during experiments of 80-h duration. Lines are smooth functions fitted to percentages of females expressing given type of behavior. RR, QQ, control groups (reared on familiar host); RQ, QR, treatment groups (reared on novel host).

noticeable differences between control and experimental groups were observed in six variables: FUE, LSN, USN, STE, MRG, and LIB. The largest group of females from each of the control groups stayed inside furrows of the upper side of experimental and new leaves. However, the percentage of females occupying the experimental leaf decreased, whereas the percentage of females occupying new leaves increased throughout the duration of the experiment. The largest group of females from both experimental groups occurred on the lower sides of new leaves, stems, leaf margins, ligules, and bases. The percentage of females that stayed on leaf margins, bases, and ligules decreased, whereas the percentage of females occupying new leaves increased throughout the duration of the experiment.

Testing Longitudinal Differences in NAB Between Familiar and Novel Hosts. There are highly significant ($P < 0.0001$ in both cases) differences in NAB between treatments (familiar versus novel host) for both host populations as calculated with GEE (Tables 2 and 3). This factor seems to be the most important variable explaining variation in NAB. For both control groups (i.e., mites reared on their familiar hosts, QQ and RR) estimated linear and quadratic coefficients were not significant, suggesting that NAB does not change over time (Tables 2 and 3). Coefficients for the experimental groups (novel host, QR, and RQ) were significant (with the exception of the linear component within RQ; Tables 2 and 3). This means that for both experimental groups (i.e., those reared on novel hosts), NAB

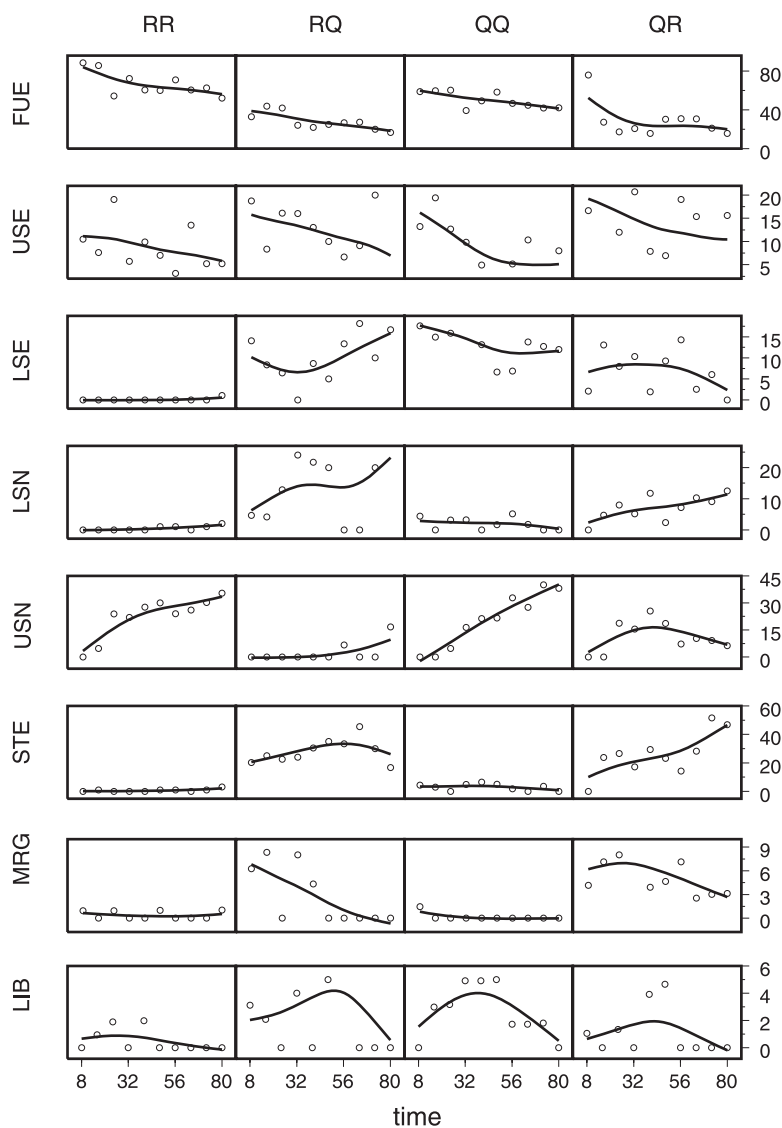


Fig. 3. Longitudinal changes in parts of the plant occupied during experiments of 80-h duration. Lines are smooth functions fitted to percentages of females found on a given part of the host plant.

changed over time. The function describing NAB is curvilinear in the time domain, with a distinct maximum, and can be approximated with a second-order degree polynomial (Fig. 4).

Discussion

We showed that the behavior of females of the grain rust mite, reared from populations collected either on

Table 2. Results of fitting GEE model to nonacceptance behavior on *Lolium* population data

Variables	Estimate	SE	Z	P
Intercept	4.54	0.04	124.81	<0.0001
Treatment (familiar versus novel host)	0.43	0.05	8.39	<0.0001
Linear component within RR	0.65	0.36	1.83	0.0676
Quadratic component within RR	-0.13	0.33	-0.39	0.6949
Linear component within RQ	-1.23	0.65	-1.89	0.0591
Quadratic component within RQ	-0.67	0.23	-2.89	0.0039
Serial autocorrelation	0.15	0.13	1.11	0.2653

Table 3. Results of fitting GEE model to nonacceptance behavior on *Elymus* population data

Variables	Estimate	SE	Z	P
Intercept	4.57	0.04	115.73	<0.0001
Treatment (familiar versus novel host)	0.39	0.06	7.02	<0.0001
Linear component within QQ	-0.34	0.28	-1.21	0.2267
Quadratic component within QQ	0.07	0.11	0.59	0.5566
Linear component within QR	0.61	0.30	2.01	0.0447
Quadratic component within QR	-1.14	0.35	-3.26	0.0011
Serial autocorrelation	0.45	0.17	2.70	0.0069

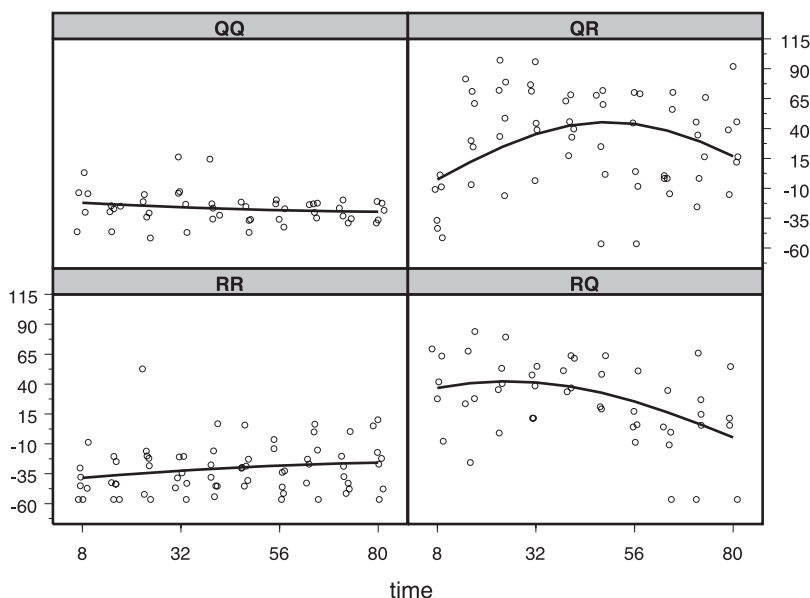


Fig. 4. GEE model fit to longitudinal development of nonacceptance behavior. Separate models, summarized in Tables 2 and 3, are fitted for both host populations. Fitted functions (second-degree polynomials) are nested within experimental groups.

ryegrass or quackgrass, clearly differs according to their hosts. Significant differences were observed in overall activity and in the part of the plant occupied between familiar and novel hosts. On familiar hosts females were not very active and showed little tendency to move (Fig. 2). Most of the time they spent lying in furrows on the upper leaf surface of experimental or newly sprouted leaves (Fig. 3). In contrast, females on novel hosts were generally more active and mobile, spending more time walking, running, and climbing over the whole plant surface including sites that are not typical for them, like leaf margins, ligules, bases, and stems (Figs. 2 and 3). In addition, they showed a high tendency toward dispersal (Fig. 2). Our findings therefore suggest that mites of each studied population can quickly distinguish between familiar and unfamiliar hosts. Recognition of the familiar host resulted in activities associated with host acceptance, i.e., seeking and occupying places suitable for feeding and egg laying, whereas detection of the novel host resulted in activities associated with host rejection, i.e., abandoning the plant, probably without any feeding.

Reaction to novel hosts by these two *A. hystris* populations was consistent with the reduced individual fitness observed previously for the same populations on the same novel hosts, whereas the accepted hosts in this study were the same ones on which these populations survived better and had higher fecundity (Skoracka and Kuczyński 2006b). Because the mites gain in fitness by discriminating between hosts, their behavior can be interpreted as adaptive for them. Furthermore, the local adaptation of ryegrass- and quackgrass-preferring populations of *A. hystris* to their familiar hosts has also been found in demographic and

morphological characters (Skoracka et al. 2002, Skoracka and Kuczyński 2006a). Thus, a positive correlation between host acceptance and performance, together with the different phenotypes exhibited by the two populations of the grain rust mite, support the hypothesis of their high host specialization and designation as distinct host races.

We observed that nonacceptance of novel hosts by *A. hystris* females from both Q and R populations decreased moderately near the end of the experiment. This was evident in the reduced activity of females, i.e., the proportion of mites walking, running, and dispersing decreased, whereas the proportion of mites lying increased (Fig. 2). We do not feel that this phenomenon can be explained by an increase of host acceptance because of adaptation by the mites to novel hosts. It is already known that the Q and R populations do not survive and reproduce on each others' hosts (Skoracka and Kuczyński 2006b). We suggest another explanation whereby nonacceptance behavior, which was high in the experimental groups, indicates that females did not occupy sites appropriate for feeding and did not assume a feeding position, so it can be concluded that they did not feed during experiment. High mobility and activity together with starvation may have caused females on novel hosts to become exhausted. Thus, what seems to be decreased nonacceptance toward the end of the experiments may in fact be a decreased ability of the mites to be mobile and active because of weakness.

In addition to differences in host acceptance between females exposed to familiar versus novel hosts, we observed various differences in behaviors between the ryegrass and quackgrass populations. Females from ryegrass that were exposed to quackgrass

promptly showed high host rejection, whereas females from quackgrass that were exposed to ryegrass initially showed less host rejection than they showed later in the experiment. This suggests that females from ryegrass came to a decision to reject the novel host more quickly than did the females from the quackgrass population. The differences between the behaviors of the ryegrass and quackgrass populations have also been displayed in the occupation of plant sites. When exposed to their familiar host, females from ryegrass occupied fewer sites compared with females from quackgrass. A lower proportion of females from ryegrass resided on the lower side of the leaf or at the base and ligule compared with females from quackgrass (Fig. 3). In summary, females from ryegrass seem to be highly specialized to the use of a few particular plant sites and they seem more decisive in host plant acceptance, whereas females from quackgrass use more plant sites and are less decisive in host acceptance. Such findings suggest that specialization of both populations of *A. hystrix* is discernible from their behavior during host plant occupation and exploitation.

Host plant preference and acceptance behaviors are thought to be very important components driving evolutionary processes that lead to host plant specialization (Jaenike 1990, Janz et al. 2001) and perhaps ultimately to speciation. The host range of many phytophagous insects is determined in part by ovipositional preferences of adult females for plants that will be suitable to their progeny (Via 1986, Thompson and Pellmyr 1991). Winged insects can actively search until they find a suitable host. Because *A. hystrix* cannot actively search for hosts, its host range is determined through acceptance or rejection of the plants on which it passively lands. Furthermore, accepted plants must sustain the reproduction of the female and provide edible both for her and her offspring. It is commonly believed that adult females of the grain rust mite reach their potential host plants by dispersal with wind currents (Nault and Styer 1969, Krantz 1973, Zhao and Amrine 1997a, 1997b). The consequences of such dispersal can be easily imagined. When a female eriophyid mite encounters any unsuitable plant, she climbs to an elevated point and adopts the dispersal position. If she is not blown away by wind currents to a suitable host, she will likely die without reproducing. However, each act of dispersal may result in encountering an unsuitable host. Thus, such wind dispersal is probably very risky for highly host-specific mites.

Therefore, one may ask how under such circumstances narrow host specialization on ryegrass and quackgrass could develop in the grain rust mite? At the current stage of knowledge, we are not able to answer this question. However, some scenarios that may explain this phenomenon can be proposed here: First, assuming wind does play a principal role in the dispersal of *A. hystrix*, mites may maximize the number of dispersing individuals through extreme fecundity. Second, wind may not play a main role in the dispersal of *A. hystrix* or it plays a role only under certain circumstances, e.g., when mite populations inhabit monocultures and the possibility of reaching a suitable

host during dispersal is higher than in heterogeneous environments. Third, other forms of transport between plants might be used more frequently than is currently known, such as a phoretic transport. In such a case, the mobility and activity of mites (especially lifting of bodies), when settled on a novel host, could be explained as activities leading to clinging to potential carriers. Transport by host-specific carriers ensures a greater possibility of finding a specific host than passive aerial transport (discussed by Sabelis and Bruin 1996). To date, few cases of eriophyoids holding on to other arthropods have been reported (Massee 1928, Gibson and Painter 1957, Shvanderov 1975, Waite and McAlpine 1992). Zhao (2000) showed that phoresy exists among eriophyoids, but it is rather rare. Fourth, perhaps the grain rust mite is not a highly mobile mite and does not change its host frequently. In this case, the mite would require adaptations to persist through phenological changes and continue development on the same or the nearest host plant. Such a strategy, i.e., the use of a diapausing form that survives on a plant during the dormant season, is successful for many eriophyoid species (Manson and Oldfield 1996). These hypotheses are not mutually exclusive and should be tested.

The results of this study show that females of ryegrass- and quackgrass-preferring populations of *A. hystrix* have the ability to discriminate between familiar and novel hosts that are both considered to be common host plants for this widespread, polyphagous, grass-feeding mite. Few similar studies have been published on herbivorous-mite host acceptance behavior. One such study on *Tetranychus urticae* (Acari: Tetranychidae) showed that the degree of acceptance of and fitness on tomato varied widely among populations of this polyphagous pest of vegetable crops (Fry 1988). That result is similar to the results presented here, although Fry (1988) compared several populations on a single host rather than two populations on their respective hosts. For a better understanding of the evolution of host specificity, it is important to recognize the decision process that leads an individual female to either accept or reject a given host. Host selection behavior is expected to be affected by information available to herbivores from plants (i.e., the plant's chemical composition and physical characteristics) (Bernays and Chapman 1994, Schoonhoven et al. 1998). The importance of chemical cues in proximate discrimination between hosts by phytophagous arthropods has been intensively studied and has provided ample evidence for the role of host plant nutritional quality and plant toxicity as sources of information leading to behavioral decisions by herbivores (Chapman 2003). Host plant quality depends on the level of primary plant metabolites and on the quantity and nature of secondary metabolites. These secondary metabolites can function as toxins, deterrents, and digestion inhibitors for herbivores that are not specifically adapted to them (Bernays and Graham 1988, Caillaud and Via 2000). Chemical and physical attributes of various plant tissues may influence a herbivore's acceptance of a host plant (Caillaud and Via

2000). Host plant structure and associated microclimate may affect behavior, e.g., host visitation and mating in certain tephritid flies (Raghu et al. 2004). Other examples show that leaf trichomes, thickness of the cuticle, and surface wax chemistry may influence host choice by herbivores (Peeters 2002). Which of these signals, and possibly others, play roles in host plant discrimination by ryegrass- and quackgrass-prefering populations of *A. hystrix* remains unknown at present and undoubtedly should be studied.

To summarize, we presented two populations of the grain rust mite, which were collected from different host taxa (ryegrass and quackgrass), that behaviorally did not accept each other's hosts and showed different behaviors when colonizing and using their proper host plants. In addition, given that both populations had lower fitness on each other's host and differed in phenotype (morphology and life history parameters) (Skoracka et al. 2002, Skoracka and Kuczyński 2006a), it can be concluded that these two populations are specialized in their host use and may be regarded as host races. However, more detailed studies including those investigating genetic variation, gene flow, and colonization performance on other hosts, are needed for a better understanding of host specialization in the grain rust mite.

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